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BIOLOGY OF THE EUCALYPT GALL-FORMING FLY, *FERGUSONINA FLAVICORNIS* MALLOCH (DIPTERA: FERGUSONINIDAE) AND ITS ASSOCIATED HYMENOPTERANS IN SOUTH AUSTRALIA, WITH A DESCRIPTION OF A NEW SPECIES OF *BRACON* (HYMENOPTERA: BRACONIDAE)

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Summary

TAYLOR, G. S., AUSTIN, A. D. & DAVIES, K. A. (1996) Biology of the eucalypt gall-forming fly *Fergusonina flavicornis* Malloch (Diptera: Fergusoninidae) and its associated hymenopterans in South Australia, with a description of a new species of *Bracon* (Hymenoptera: Braconidae). *Trans. R. Soc. S. Aust.* **120**(4), 131-146, 29 November, 1996.

Galls initiated by the association of *Fergusonina flavicornis* Malloch (Insecta: Diptera: Fergusoninidae) and *Fergusobia* sp. (Nematoda: Sphaerulariidae) on *Eucalyptus camaldulensis* Dehnh. at Goolwa, South Australia were monitored during a single, late summer generation for emergence of flies and associated Hymenoptera. The morphology of the galls is described for the first time. A total of 12 hymenopteran species was reared from galls, twice the number previously recorded from *Fergusonina/Fergusobia* galls. There was a strong positive correlation between emergence of flies, combined totals of flies and wasps and gall size. *Bracon fergusoninus* sp. nov., a probable primary parasitoid of *F. flavicornis* larvae, is described. Notes on the biology and taxonomy of each hymenopteran species are presented along with an illustrated key to their identification.

KEY WORDS: *Eucalyptus*, gall-forming, *Fergusonina*, Diptera, Fergusoninidae, parasitic Hymenoptera, Braconidae, *Bracon*, *Fergusobia*, Nematoda, Sphaerulariidae.

Introduction

The biology of gall-associated Hymenoptera is fundamentally complex and it is often extremely difficult to determine the true relationships of species (Bouček 1988; Gough & McMahon 1988; Naumann 1991; Schönrogge *et al.* 1996). For instance, galls may contain a range of biologically different Hymenoptera, viz., primary parasitoids, facultative and obligate hyperparasitoids and inquilines. The biology of the latter group is particularly difficult to unravel. Inquilines are species that live inside galls of other cecidogenic insects and are phytophagous for all or some of their larval development. They often kill the primary gall-forming species at an early stage of gall development and then increase the size of the gall, thereby making it difficult to determine whether or not the species concerned is indeed an inquiline or the primary gall-former. Other inquilines apparently invade galls and feed on their tissues without disrupting the primary cecidogenic species.

One of the most complex gall associations known is that between *Fergusonina* spp. (Insecta: Diptera: Fergusoninidae) and *Fergusobia* spp. (Nematoda: Tylenchida: Sphaerulariidae) in galls on Myrtaceae (Fisher & Nickle 1968; Harris 1982; Davies & Lloyd 1996). However, the only detailed study of the biology and phenology of *Fergusonina* Malloch flies is that of Currie (1937), who commented on the possible role of hymenopterans and other gall inquilines in the seasonal fluctuations of fly populations. This study showed that numerous wasps were associated with *Fergusonina/Fergusobia* flower bud galls. Although Currie (1937) examined the biology of this system, the taxonomic knowledge at the time was limited and the biology of the species involved was not well understood.

This paper reports on a study of the leaf galls of *Fergusonina flavicornis* Malloch associated with an undescribed species of *Fergusobia* Currie and the associated guild of hymenopterans from galls on *Eucalyptus camaldulensis* Dehnh. at Goolwa, South Australia. Information is presented on gall morphology, the phenology of the fly and wasps, the probable biology of the hymenopteran species involved, their taxonomy, and the relationship between numbers of flies and wasps and gall size. A new species of *Bracon* F., thought to be a primary parasitoid of *Fergusonina*, is described and an illustrated key to the 12 gall-associated hymenopterans is presented. This information is compared with Currie's (1937) study and is discussed in relation to the inherent difficulties in determining the biology of gall associated wasps.

Materials and Methods

Seven mature galls on an ornamental, 4 m high *E. camaldulensis* sapling at Goolwa, (35°31' S,

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138°46′ E) South Australia were caged with muslin in early March, 1995, preceding emergence of adult *F. flavicornis* and other gall occupants, and periodically monitored until after senescence of the gall and when flies and wasps ceased to emerge. Any insects that had emerged at each sampling time were collected, identified and counted. Galls were dried and weighed to compare gall mass with total insect emergences. For observations on gall development and morphology, young fresh galls were sliced open in water by a series of transverse cuts. Abbreviations used are: ANIC (Australian National Insect Collection, CSIRO, Canberra) and WARI (Duncan Swan Insect Collection, Waite Campus, The University of Adelaide). Voucher material of *F. flavicornis* has been lodged at ANIC and WARI and material of all hymenopteran species is deposited in WARI.

Results and Observations

Distribution and host plant association

Fergusonina flavicornis was the only dipteran reared from an ornamental specimen of *E. camaldulensis* at Goolwa. Similar galls have been collected by us from several other South Australian localities from naturally-occurring *E. camaldulensis* near Verdun and near Milang, and from this same host in the Adelaide suburbs of Hyde Park, Rose Park, Tusmore and Urrbrae. *Fergusonina flavicornis* was described from a single female specimen from Sydney, NSW (Malloch 1925). Larvae, males and galls have remained undescribed to date. This is the first host plant record for the species and first description of the gall (see below). We have also collected all life history stages of *F. flavicornis* and the associated, undescribed species of *Fergusobia* and plan to discuss these in a separate publication.

Gall morphology and formation

The galls of *F. flavicornis* are formed from terminal leaf buds, mature galls (Fig. 1) being bulbous structures, mostly ovoid in longitudinal cross section, 18-50 mm in length by 12-20 mm in diameter. Mean dry weight of mature galls was 2.22 ± 1.45 g (range 0.89-5.16 g, n = 7). Galls appear to consist of a single leaf bud comprising a number of leaves, with the ventral surface of the outermost forming the external face of the gall. The growth of these outer leaves sometimes continues unaffected beyond the gall proper, either running along the side of the gall or emerging as normal leaf tissue beyond its apex. The stem supporting the gall usually develops a bend just before its insertion in the base of the gall. Transverse sections showed that the galled tissue is soft, consisting of parenchymatous tissue, and that *F. flavicornis* larvae develop in discrete cavities. These are oval in longitudinal outline and distributed throughout the gall. The cavities are lined with plant cells which are paler in colour than the parenchyma cells between them. *Fergusobia* nematodes are found in the cavities with the fly larvae.

For the generation of *F. flavicornis* which began in late March, small, recently initiated galls were observed. Four of these were collected and dissected and the development of others was monitored during the study. Full gall size was reached on the tree in two to four weeks from gall initiation. The following observations were made on the dissected galls. The smallest gall, 8 mm in length contained 20 spindle-shaped *F. flavicornis* eggs (Fig. 2) within which developing larvae could be seen. It contained many parthenogenetic and juvenile nematodes and some nematode eggs. At this stage of development no cavities were present. Another, 10 mm long, contained several eggs, a few first instar larvae of *Fergusonina* and many parthenogenetic nematodes and eggs. Some fly larvae were found within cavities, the small cavities being ringed with many white cells. A 12 mm long gall contained first and second instar larvae of *Fergusonina*, all within cavities, and many parthenogenetic nematodes and eggs. The largest gall, about 30 mm in length, contained first and second instar fly larvae within

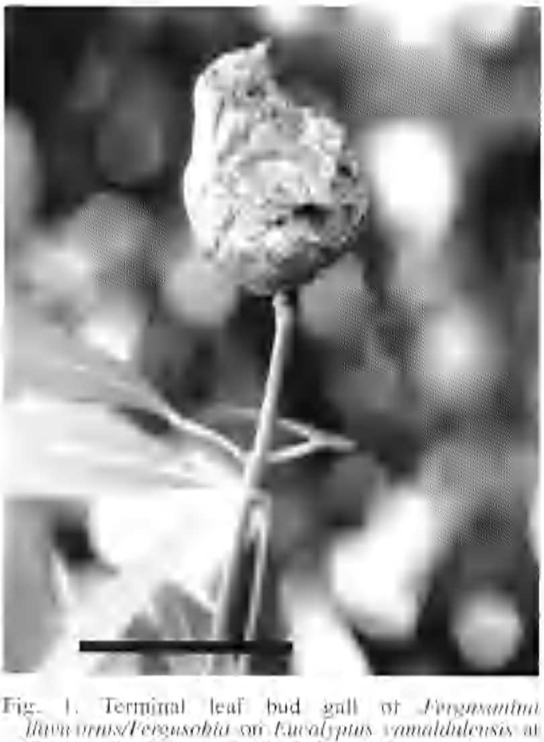


Fig. 1. Terminal leaf bud gall of *Fergusonina flavicornis/Fergusobia* on *Eucalyptus camaldulensis* at Goolwa, South Australia. Scale bar = 25 mm.

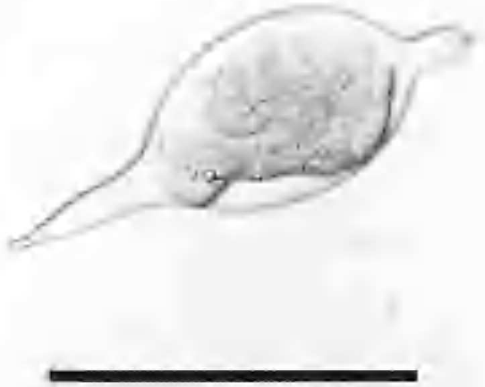


Fig.2. Egg of *Fergusonina flavicornis* from a terminal leaf bud gall from *Eucalyptus camaldulensis* at Goolwa, South Australia. Scale bar = 0.25 mm.

well-defined cavities, none of which was ringed with white cells. It contained many parthenogenetic female, juvenile and male nematodes and eggs. The three larger galls each contained brown 'streaks', running from the centre to the outer edges, apparently formed by the darkening of intact plant cell walls. These observations on the process of gall induction indicate that *F. flavicornis* and nematodes are always present together and that both fly larvae and nematodes continue to develop, thus increasing the size of the cavities. We have not been able to determine whether gall initiation requires both species to be present or if only one is required. Given that nematodes are present in the early gall matrix prior to hatching of fly eggs, it is possible that initially, gall tissue is produced in response to nematode secretions (see Discussion).

Egg and dorsal shield of Fergusonina flavicornis

The egg of *F. flavicornis* is spindle-shaped and tapers to a short, blunt 'pedicel' at the micropylar (anterior) end and to a somewhat longer, tapered process at the other end (Fig. 2). The egg is 0.65 ± SE 0.06 mm long by 0.26 ± SE 0.03 mm wide (n = 4). It is larger than the egg of *F. nicholsoni* Tonnoir which was described and illustrated by Currie (1937).

Second and third instar larvae of most described species of *Fergusobia* have a more or less elaborate dorsal shield (Currie 1937). In *F. flavicornis* it consists of a sclerotised modification to the second and third thoracic segments and first abdominal segment comprising a plate with sometimes three, mostly four and rarely five anteriorly projecting prongs arising from the third thoracic segment. The structure of the shield is similar to that depicted for *F. lockharti* Tonnoir by Currie (1937). Its function is implicated in feeding and the enlargement of gall cavities (see Discussion). Indeed many pellets of plant material were found in the gall cavities often adhering to the dorsal shield. Faecal material within the gall cavities was not observed.

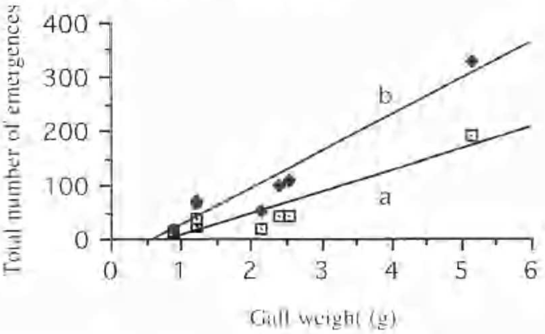


Fig. 3. Relationship between total number of emergences per gall for (a) *Fergusonina flavicornis* alone, and (b) *F. flavicornis* plus associated Hymenoptera versus gall weight (in grams), reared between 5 March and 30 April 1995 from *Eucalyptus camaldulensis* at Goolwa, South Australia.

Emergence and Phenology of Fergusonina *and associated Hymenoptera*

Galls collected in late February 1995 contained only larval stages of *F. flavicornis* but pupae were present soon after. Galls were caged in the field on 5 March (day 0) and the first adult *F. flavicornis* had emerged by day 3. Adult flies continued to emerge for about the next 40 days, peaking around day 18 (23 March) (Fig. 4a). The 370 adult *F. flavicornis* that emerged from the caged galls had a sex ratio slightly biased in favour of males (1: 1.2). Further, the number of flies that emerged had a positive relationship with gall size (measured as dry gall weight) (Fig. 3, line b). However, the regression against gall size was steeper for flies plus associated Hymenoptera (Fig. 3, comparing lines a and b), and the correlation slightly better ($r^2 = 0.91$ versus 0.87), compared with flies alone. The reason for this is not clear but, presumably, gall size is a reasonable estimate of available food and so for a given gall there must be a limit to the number of flies it can support. However, all galls surveyed (Table 1) contained some Hymenoptera, and these individuals, whether they are phytophagous, parasitic on *F. flavicornis*, or both (inquilines), will have displaced or killed flies that otherwise would have completed development and emerged. Hence, the steeper slope of the regression line for flies plus Hymenoptera represents what is a closer estimate for the carrying

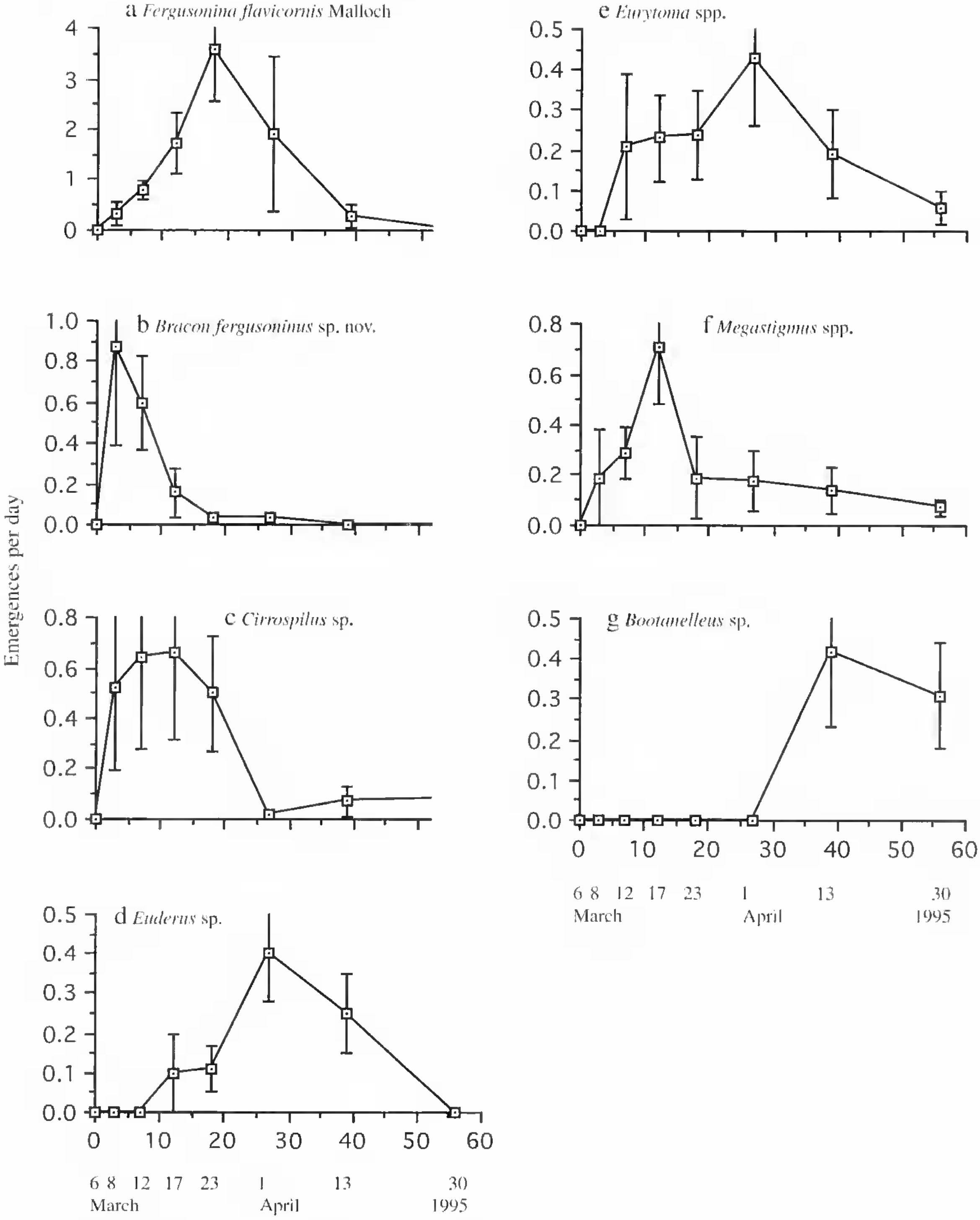


Fig. 4. Number of emergences per day for *Fergusonina flavicornis* (4a) and the six most abundant Hymenoptera (4b-4g) reared from galls between 5 March (day 0) and 30 April 1995 (day 56) on *Eucalyptus camaldulensis* at Goolwa, South Australia. The standard errors around the means are different for each species because the number of galls in which they occurred was also different (see Table 1).

TABLE 1. *Total emergences from 3 March - 30 April, 1995 of* Fergusonina flavicornis *and associated hymenopteran spp. from* Fergusonina/Fergusobia *galls on* Eucalyptus camaldulensis *at Goolwa, S. Aust.*

	Gall number							
Species	1	2	3	4	5	6	7	Total
Fergusonina flavicornis Malloch	19	24	12	44	44	189	38	370
Bracon fergusoninus sp. nov.	2	17	0	0	1	10	1	31
Poecilocryptus spp.	0	1	0	1	2	2	0	6
Cirrospilus sp.	6	7	1	4	21	37	13	89
Euderus sp.	3	1	0	9	8	15	8	44
Pediobius sp.	0	0	0	1	0	0	0	1
Eurytoma spp.	14	11	3	11	4	25	3	71
Coelocyba nigrocincta Ashmead	0	5	1	2	2	5	0	15
Ditropinotella sp.	0	0	0	0	4	3	2	9
Megastigmus spp.	6	5	2	19	12	30	1	75
Bootanelleus sp.	2	0	0	17	2	12	0	33
Total parasitoids	33	47	7	64	56	139	28	374

capacity of a gall in terms of food resources, compared with that for flies alone.

The composition of the hymenopteran species that emerged from caged galls varied in all cases, except between galls 5 and 6 which yielded the same species (Table 1). Galls contained an average of seven species (range = 4-9), with no gall containing all species (note that in Table 1 species for each of *Poecilocryptus*, *Eurytoma* and *Megastigmus* have been combined). The biology of the individual hymenopteran species in this guild is discussed below. Of these, several were reared in sufficient numbers (> 30 individuals) to examine their pattern of emergence (Fig. 4b-g). *Bracon fergusoninus* sp. nov., *Cirrospilus* sp. and *Megastigmus* spp. all had a peak in their emergence prior to that of *F. flavicornis*. For *B. fergusoninus*, this peak occurred at the beginning of the study (day 3) and virtually all individuals had emerged prior to the peak of *F. flavicornis* on about day 18, while *Cirrospilus* sp. and *Megastigmus* spp. continued to emerge from galls until day 56, albeit in low numbers for most of this time. *Euderus* sp. and *Eurytoma* spp. had a broad range of emergence times, beginning prior to the maximum in *F. flavicornis* (day 18), peaking at about day 27 and continuing to, or almost to, day 56 when the study was terminated. In contrast, *Bootanelleus* sp. did not start emerging from galls until 21 days after the peak in *F. flavicornis*. Emergence of this species reached a maximum about day 39 and some individuals were still emerging from galls up to day 56. Of the other hymenopteran species that were reared in low numbers (<30 individuals), the emergence of *C. nigrocincta* (days 1-27) straddled the peak for *F. flavicornis*. *Poecilocryptus* spp. (6 individuals from days 23-39) and *Ditropinotella* sp. (9 individuals from days 28-56) emerged well after *F. flavicornis*, while the single specimen of *Pediobius* sp. emerged between days 13 and 18 (18-23 March).

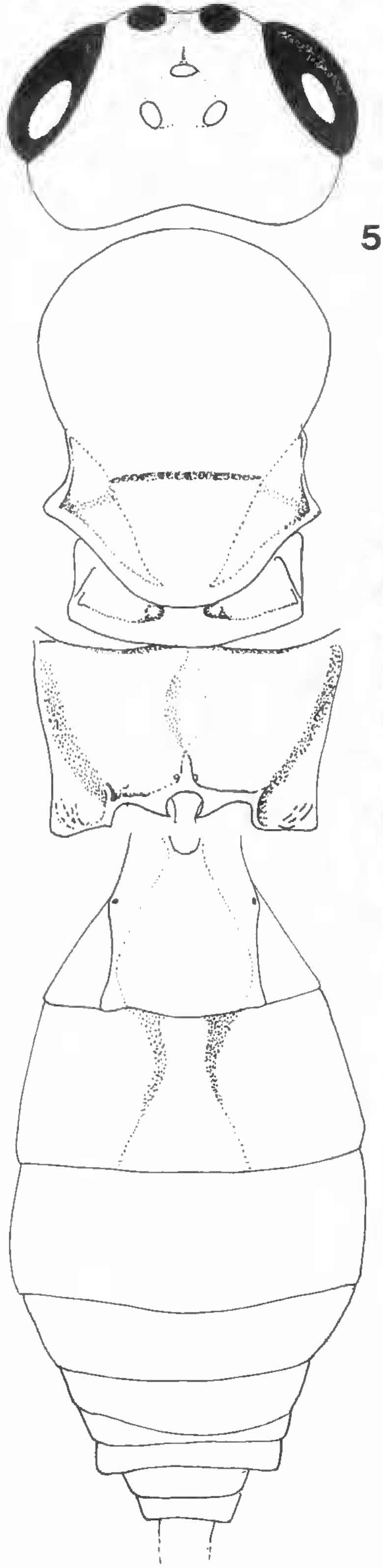
Taxonomy and biology of Hymenoptera associated with Fergusonina

During the study 12 species of Hymenoptera were reared from *Fergusonina/Fergusobia* galls on *E. camaldulensis*. This section describes some aspects of the biology of the species concerned and speculates on other aspects of their association, based on information available for other related species. Notes are provided on their taxonomy, including the description of a new species, and an illustrated key is provided to identify the 12 species.

Family Braconidae
Bracon fergusoninus sp. nov.
(FIGS 5-8)

Holotype: ♀, South Australia, Goolwa, 6-8.iii.1995, G. Taylor & K. Davies, reared from *Fergusonina* galls on *Eucalyptus* sp. (ANIC).
Paratypes: 8 ♀♀, 18 ♂♂, same data as holotype except some with dates as follows 9-12.iii.95, 13-17.iii.95, 24.iii.-1.iv.95 (ANIC, WARI).

Female
Size: Length 2.4-2.6 mm (excluding ovipositor).
Colour: Head, scutum, pronotum, legs and anterior two-thirds of metasoma yellow-brown to orange-brown; antennae, eyes, posterior parts of mesosoma and metasoma, distal half of hind legs, proximal, mid and hind coxa and ovipositor sheaths black; sometimes area around ocelli and posterior margin of scutum darker; wings evenly infuscate.
Head: In anterior view face half width of head; eyes moderately bulbous, hairless; face, gena and mandibles evenly covered with long hairs; in dorsal view vertex, dorsal temples and lateral frons with



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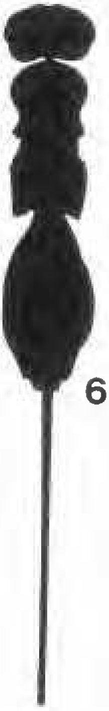

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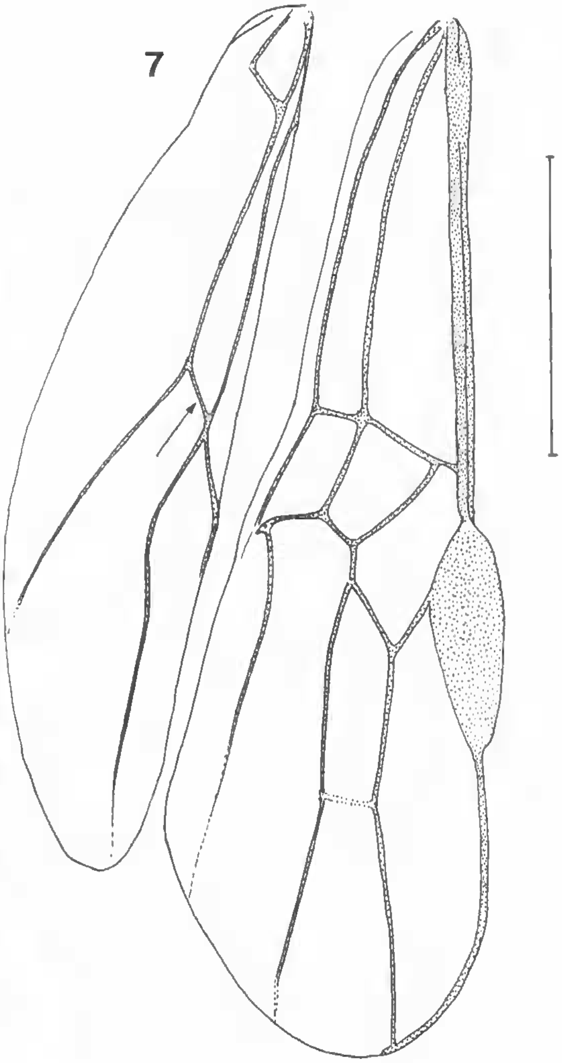

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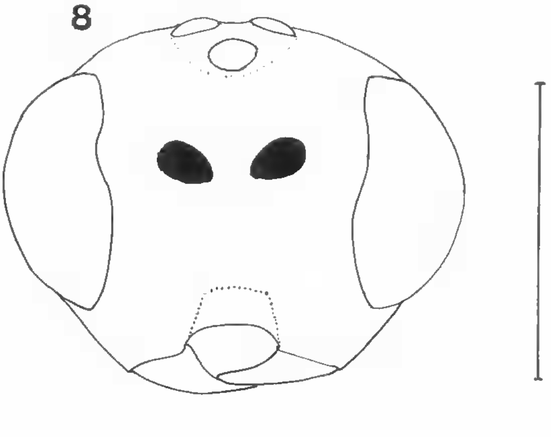

long hairs; in lateral view lower temple glabrous; antennae slightly longer than body; flagellomeres all longer than wide.

Mesosoma: Scutum and scutellum smooth, shiny, with a few long sparse hairs on posterior parts of each tergite, scutum with sparse hairs along lateral margin and along notauli; notauli indicated by faint depressions more prominent in posterior half; scutellar suture slightly depressed and curving posteriorly, comprising 12-14 foveate punctures; dorsal and lateral scutellum delimited by row of longish hairs; propodeum with medial longitudinal carina in posterior one-third, faintly depressed in anterior midline, with sparse long hairs in lateral part; in lateral view pronotum and mesopleuron smooth and mostly hairless; epicnemial area covered with long hairs; metapleuron covered with long hairs, smooth in dorsal half, faintly rugose in postero-ventral part; legs evenly and densely setose except for outer surfaces of coxae; fore wing with 1M and 1-Rs+M faintly bowed, 2-Rs straight; 3-CU1 evenly curved; 2nd submarginal cell elongate, sides (3-Rs and 2-M) almost parallel, 1st discal cell moderately elongate (1-Rs+M 2.8 x length of m-cu).

Metasoma: Mostly smooth throughout; sclerotised part of T1 slightly longer than wide, lateral margins with long sparse hairs, postero-medial lobe of T1 broad, faintly longitudinally striate along posterior margin, delimited by shallow lateral furrows which are percurrent to base of T1; T2 with broad medial longitudinal carina in anterior half with a few striae either side, postero-medial area very faintly raised and triangular; T2 and T3 subequal in length and comprising about one-third length of metasoma, with sparse long hairs in lateral parts; T3-T5 about three-quarters length of T2-T3, with transverse row of long hairs and at lateral margins; ovipositor and sheaths slightly longer than body, sheaths with even covering of long hairs, slightly longer than diameter of sheaths.

Male

Differing from female as follows: Length 2.3-2.6 mm; body generally narrower and more elongate, particularly posterior mesosoma and T1; scape and often proximal one-quarter of antennae brown, legs with same colour pattern but yellower; wings narrower.

Comments

This is a very large genus in Australia of which few species have been described. Primarily, members of the genus are parasitic on lepidopteran larvae but they have also been recorded from Coleoptera, Diptera and leaf-mining pergid sawflies (Quicke 1988; Quicke & Ingram 1993; Austin & Faulds 1989). Other than one unsubstantiated record of a *Bracon* species being reared from a gall-forming homopteran (Chadwick & Nikitin 1976), this is the first record of an Australian species being reared from a plant gall. Studies on the biology of numerous species overseas and from Australia indicate that all members of the genus are solitary primary ectoparasitoids. Given this, and that *B. fergusoninus* was reared in moderately large numbers from five of seven galls during the project (Table 1), this species is most likely to be parasitic on *Fergusonina* larvae. Previously, Currie (1937) reported rearing an unknown braconid from galls of *Fergusonina* in the Canberra area, and this may be the same species as decribed here. However, there is apparently no voucher material available from Currie's study in the ANIC or elsewhere. Further, Currie (1937) found this braconid "to feed indiscriminately on gall tissues and fly larvae." We have been unable to confirm Currie's observations but, if this species is a facultative feeder on gall tissue, it will be only the fourth record of phytophagy in the Braconidae in the world (Austin & Dangerfield unpub.), and the first for the subfamily Braconinae.

Bracon fergusoninus differs from other described Australian *Bracon* species in the form of the medial propodeum, shape of T1, sculpturing on T2, length of the ovipositor, and its colour pattern. It is easily identified from other parasitoids associated with *Fergusonina/Fergusobia* galls by its complete wing venation (Fig. 7), circular and depressed (cyclostome) clypeus (Fig. 8), elongate ovipositor (Fig. 6), and orange and black colour pattern.

Family Ichneumonidae
Poecilocryptus spp.
(FIGS 9-11)

This genus belongs to an unusual subfamily, the Labeninae, in that it represents one of the most plesiomorphic groups of ichneumonids and has a Gondwanan distribution (Gauld 1983, 1984; Gauld & Holloway 1986). *Poecilocryptus* has been postulated to be phytophagous on the basis of the structure of the mandible (Short 1978) and it has previously been reared from galls on *Acacia* and *Eucalyptus* (Gauld & Holloway 1986) and, more recently, from *Banksia* (Austin & Dangerfield

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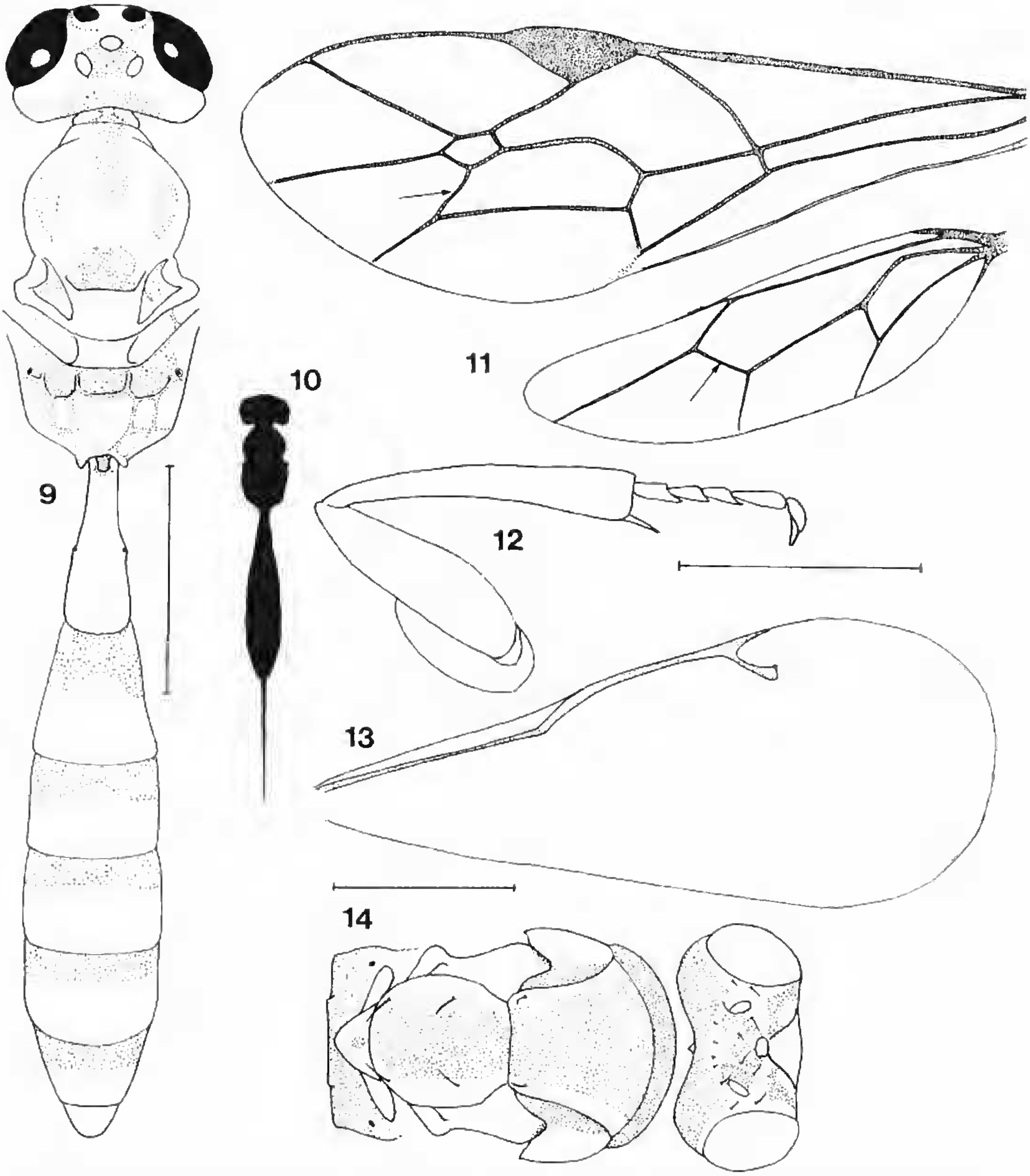
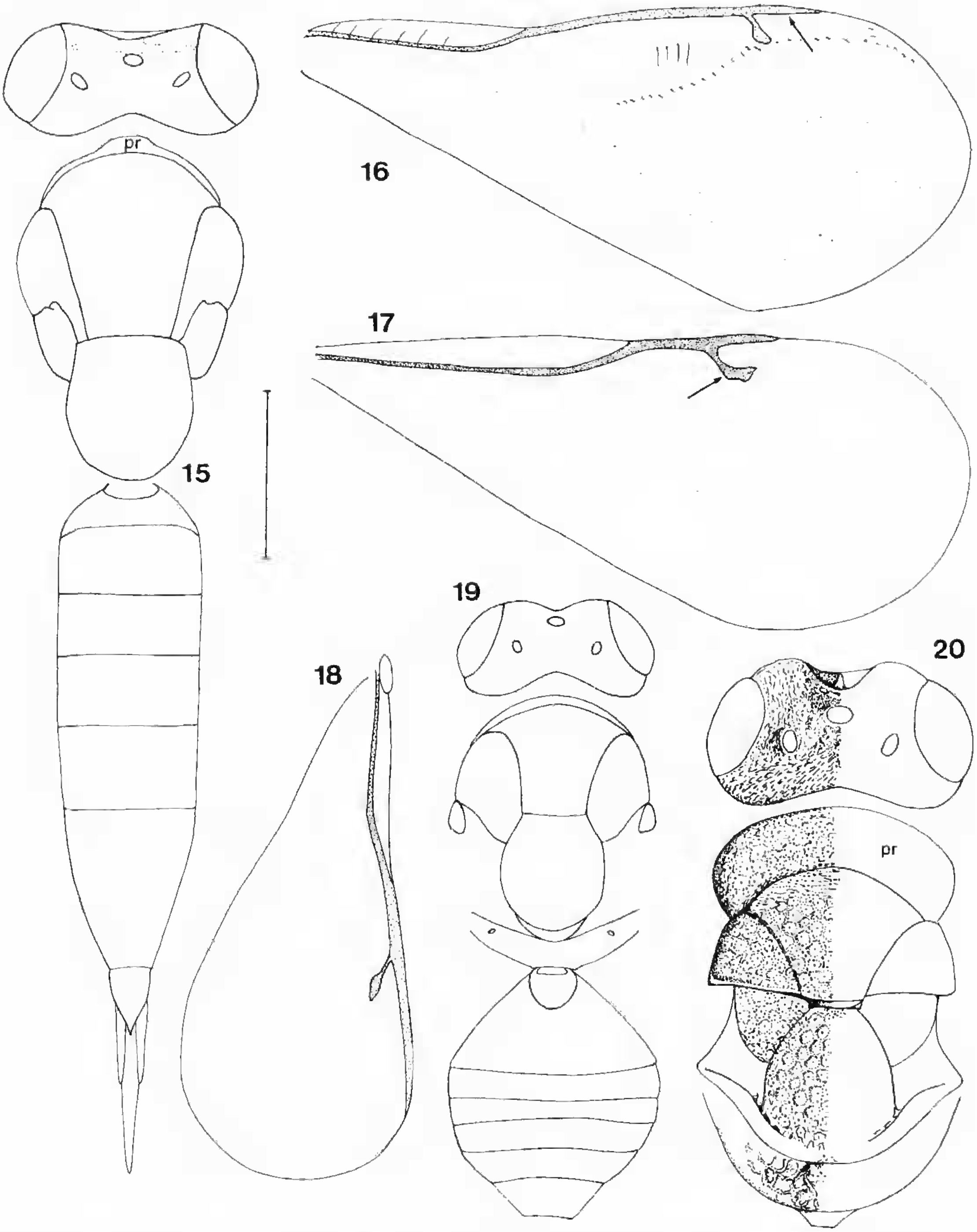
Figs 5-8. *Bracon fergusoninus* sp. nov. ♀ 5. Dorsal habitus (not showing ovipositor). 6. Silhouette of dorsal body showing length of ovipositor. 7. Fore and hind wings (vein r-m arrowed in hind wing). 8. Anterior view of head showing circular clypeus. Scale bars 0.5 mm 5; 1.0 mm 7; 0.5 mm 8.

unpub.). However, only very few specimens have ever been reared, as is the case here (i.e. six specimens from four galls - Table 1), indicating that the genus is more likely to be a parasitoid or inquiline than a primary gall-former. Surprisingly, two of the four known species of *Poecilocryptus*, *P. nigromaculatus* Cameron and *P. galliphagus* Gauld & Holloway, are here associated with *Fergusonina/Fergusobia* galls. Both species have previously been collected from the eastern part of the continent, Queensland to Tasmania, but both are recorded here from South Australia for the first time. *Poecilocryptus nigromaculatus* has been reared from anthribid and chalcid galls on *Acacia longifolia* and eriococcid



Figs 9-14. 9-11. *Poecilocryptus nigromaculatus* Cameron. 9. Dorsal habitus, ♂ (extent of black markings indicated by stippling). 10. Silhouette of dorsal body of ♀ showing length of ovipositor. 11. Fore and hind wings of ♂ (vein 2mcu arrowed in fore wing and vein r-m arrowed in hind wing). 12-14. *Cirrospilus* sp. ♀. 12. Hind leg. 13. Fore wing. 14. Dorsal head and mesosoma (extent of metallic green markings indicated by stippling). Scale bars = 1.25 mm 9, 11; 0.5 mm 12-14.



Figs 15-20. 15, 16, *Euderus* sp. ♀. 15. Dorsal habitus (pr = pronotum). 16. Fore wing (postmarginal vein arrowed). 17, 20, *Eurytoma* sp. 17. Fore wing (stigmal vein arrowed). 20. Dorsal head and mesosoma (pr = pronotum). 18, 19, *Pediobius* sp. ♀. 18, Fore wing. 19. Dorsal head and mesosoma. Scale bar = 0.5 mm.

galls on *Eucalyptus*, while *P. galliphagus* has been associated with unknown galls on *E. delegatensis* and *E. pauciflora* (Gauld & Holloway 1986). *Poecilocryptus* spp. are distinctive compared with other parasitoids in the guild because of their large size (approximately 10 mm excluding ovipositor) and wing venation (Fig. 11). Although the two species are very similar to each other, they can be separated by the colour of the hind femur and length of the ovipositor.

Family Eulophidae
Cirrospilus sp.
(FIGS 12-14)

Members of this very large and taxonomically difficult cosmopolitan genus are relatively small in size and are often brightly coloured with metallic markings, as is the species here. Different species have been reared as primary parasitoids or as facultative or obligate hyperparasitoids from leaf-mining and gall-forming insects. Thumlert and Austin (1994) recorded four species associated with the mines of *Phylacteophaga* on eucalypts in South Australia which, in the case of the dominant species, *C. marginiventris* Girault, was shown to be a facultative hyperparasitoid of *Bracon* and other chalcidoids. The biology of the species here is unclear and it could be either a primary parasitoid on *Fergusonina* larvae or facultatively hyperparasitic on one or more of the gall-associated Hymenoptera. It was the most abundant parasitoid encountered during the study and it was recorded from all seven galls (Table 1). The species is close to *C. occipitis* Girault but differs in the colour pattern of the dorsal mesosoma, and thus may represent a new species. Within the parasitoid guild associated with *Fergusonina/Fergusobia* galls, it can be easily identified based on the form of the fore wing venation (Fig. 13), colour pattern and shape of the body (Fig. 14).

Euderus sp.
(FIGS 15, 16)

Like *Cirrospilus*, this is a large genus whose members are difficult to identify. Extralimital host records indicate that *Euderus* are parasitoids of lepidopteran larvae or are hyperparasitoids, particularly of Braconidae (Bouček 1988). The association of the species reared here from *Fergusonina/Fergusobia* galls is the first biological information recorded for the genus in Australasia. Given that species overseas have been reared from Braconidae, it is possible that this species is hyperparasitic on *B. fergusoninus*. This proposal is supported at least in part by the fact that *Euderus* sp. was reared from galls that also yielded individuals of *B. fergusoninus* (Table 1), and that no other hymenopterans in the same galls are large enough in body size to provide sufficient food for the development of *Euderus* larvae (with the exception of *Poecilocryptus* which was too rare). In the parasitoid guild associated with *Fergusonina/Fergusobia* galls, *Euderus* sp. is easily separated from other species by its metallic blue-green colour, elongate body (Fig. 15), mesosoma with very fine reticulate-punctate sculpturing and fore wing with postmarginal vein about as long as stigmal vein (Fig. 16).

Pediobius sp.
(FIGS 18, 19)

Members of this genus are known to be primary and hyperparasitoids of eggs, pupae and sometimes larvae of various insects, mainly Lepidoptera, Coleoptera, Diptera and Hymenoptera (Bouček 1988). Several species have been reared from leaf-feeding insects on eucalypts (e.g., *Uraba lugens* Walker and *Phylacteophaga froggatti* Riek - Austin & Allen 1989; Thumlert & Austin 1994) and various leaf-mining Diptera (Bouček 1988), but apparently none has been reared from gall-associated hosts. The species here was recorded by only a single specimen (Table 1). Although its biology is not known, this very low abundance would indicate that it is probably a hyperparasitoid on another hymenopteran in the *Fergusonina/Fergusobia* guild. *Pediobius* sp. can be easily separated from the other parasitoids recorded by its relatively short compact body (Fig. 19), black colour, very finely reticulate dorsal mesosoma, and elongate postmarginal vein (Fig. 18).

Family Eurytomidae
Eurytoma spp.
(FIGS 17, 20)

This is a very large genus in Australia containing species with divergent biologies. Species can be phytophagous, facultatively parasitic, obligatorily parasitic or hyperparasitic (Bouček 1988). In Australia, the majority of species are postulated to fall into the latter two categories, but the generic classification is not well understood and species belonging to apparently closely related genera and/or species groups are known to be either phytophagous or parasitic. A number is known to be ectoparasitic on gall-forming insects or hyperparasitic through ichneumonid and braconid cocoons (Bouček 1988). Currie (1937) reported one species of *Eurytoma*, *E. "varirufipes"*, to be phytophagous in *Fergusonina* galls near Canberra (*varirufipes* is an unpublished manuscript name - see Dahms 1986; Bouček 1988). Unfortunately, we have not been able to confirm the biology of the species encountered in this study by direct observation. One of them (see below) may be the same species as recorded by Currie (N.B. no voucher material is available from his study) and therefore possibly be phytophagous (see Discussion), or they could be different species and be parasitic on *Fergusonina* larvae or on one of the other hymenopterans in the guild, possibly *B. fergusoninus* sp. nov. The species here was recorded from all the galls surveyed and was the third most abundant hymenopteran in the *Fergusonina/Fergusobia* guild (Table 1).

Eurytoma often display intraspecific morphological variability and are therefore difficult to separate at the species level. The material reared here varies slightly in size, colour, pilosity and sculpturing and may represent more than one species. The genus can be easily separated from other parasitoids in the guild based on the shape of the pronotum, dorsal sculpturing pattern (Fig. 20), and wing venation (Fig. 17). The sexes are highly dimorphic with males being smaller, having a disproportionately smaller metasoma, and asymmetrical pilose antennae.

Family Pteromalidae

Coelocyba nigrocincta Ashmead

(FIGS 23, 24)

This species and all members of the genus are probably inquilines of hymenopteran and dipteran gall-formers on *Acacia* and *Eucalyptus* (Bouček 1988). Previously, *C. nigrocincta* has been reared from the galls of the phytophagous pteromalids *Trichilogaster* and *Perilampella* (Noble 1940, 1941) and, in the latter case, has been proved to be an inquiline, i.e., it kills the resident cecidogenic wasp and forms its own cells to feed on the gall tissue. The species was originally described from material reared from "agromyzid galls on *Eucalyptus corymbosa*" (identified by Bouček (1988) as *Fergusonina* galls) in Sydney (Ashmead 1900), and was subsequently recorded from *Fergusonina/Fergusobia* galls as an obligate parasitoid in the Canberra area by Currie (1937). Specimens in ANIC were collected from galls on *E. camaldulensis* at Alice Springs, NT and *E. sieberi* L. Johnson and *E. amygdalina* Labill. at Bicheno, Tas. (I. D. Naumann pers. comm.). We have been unable to confirm its biology in this study, but clearly it is most likely to be an inquiline or primary parasitoid of *Fergusonina*. *Coelocyba nigrocincta* was reared only in moderate numbers here but it was recorded from five of the seven galls surveyed (Table 1). It is apparently distributed along the east coast of Australia from north Queensland to Tasmania, but this seems to be the first record of the species from South Australia. *Coelocyba nigrocincta* can be easily separated from other parasitoids associated with *Fergusonina/Fergusobia* galls by its elongate stigmal vein, short ovipositor and distinctive bright yellow body and metasoma with black transverse stripes (Fig. 23).

Ditropinotella sp.

(FIG. 26)

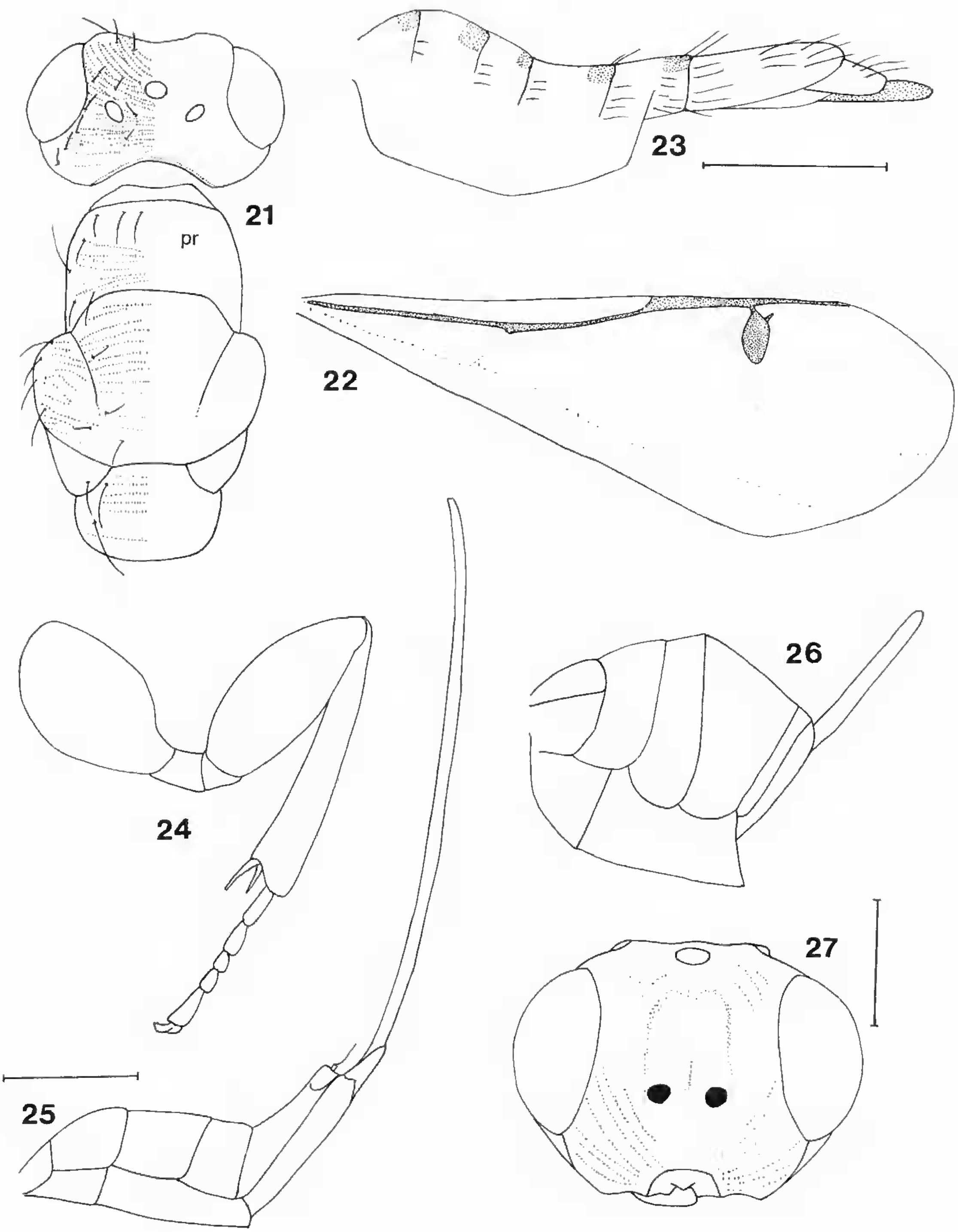
Members of this genus have previously been treated under the Torymidae or as miscogasterine pteromalids, but most recently they have been placed in their own subfamily, Ditropinotellinae, within the Pteromalidae (Bouček 1988). Previously, they have been reared from *Apiomorpha* galls on *Eucalyptus* and unknown galls on *Eucalyptus*, *Acacia*, *Casuarina* (Bouček 1988) and a number of other plants. The biology of the genus is poorly known. However, Currie (1937) reported *D. compressiventris* Girault to be phytophagous within *Fergusonina/Fergusobia* galls in the Canberra area. During this study, only nine individuals were reared from three galls (Table 1) and, based on these numbers, the species is more likely to be an inquiline or parasitic on one or more gall inhabitants. We have not been able positively to identify the species here as *D. compressiventris*, primarily due to morphological variability among species in the genus (Bouček 1988). However, it can be easily distinguished from the other parasitoids in the guild by its bright metallic green body, laterally compressed metasoma, and exserted ovipositor (Fig. 26).

Family Torymidae

Megastigmus spp.

(FIGS 21, 22, 25)

The Megastigminae are best characterised by their large, knob-like fore wing stigma and elongate ovipositor of the female. The genus *Megastigmus* is large and taxonomically difficult in Australia, with more than 40 described species. As well, its members have diverse biologies in that apparently closely related species can be phytophagous, cecidogenic, inquilines or parasitic, although the detailed biology of no Australian species has been confirmed (Bouček 1988). Various species have been reared from dipteran galls on *Asterramulosus*, *Apiomorpha* (Eriococcidae) on *Eucalyptus*, *Bruchophagus* (Eurytomidae) galls on *Eremocitrus*, *Trichilogaster* (Pteromalidae) galls on *Acacia*, as well as unknown galls on numerous native plants (Bouček 1988). Two species, *M. quinquesetae* Girault and *Megastigmus* sp., were reared from *Fergusonina/Fergusobia* galls in the Canberra area by Currie (1937), and were reported by him to be phytophagous. We have been unable to confirm Currie's identification of these species, or to show



Figs 21-27. 21, 22, 25, *Megastigmus* sp. ♀. 21. Dorsal head and mesosoma (pr = pronotum). 22. Fore wing. 25. Lateral view of metasoma and ovipositor. 23, 24, *Coelocyba nigrocincta* Ashmead ♀. 23. Lateral view of metasoma (extent of black markings indicated by stippling). 24. Hind leg. 26. *Ditropinotella* sp. ♀. Lateral view of metasoma and ovipositor. 27. *Bootanellus* sp. ♀. Anterior view of head. Scale bars= 0.5 mm 21-26; 0.25 mm 27.

that they are indeed phytophagous. The number of individuals obtained for the two species reared here was pooled because of initial problems in separating them taxonomically. Combined, they were reared from all seven galls surveyed and occurred in large numbers (Table 1), being the second most abundant genus present in the guild.

Megastigmus can be easily distinguished from the other *Fergusonina/Fergusobia* gall-inhabiting Hymenoptera by their spot-like fore wing stigma (Fig. 22), bright yellow colour with some dark markings, and the length of the ovipositor (Fig. 25). From each other they can be separated by the colour of the metasoma. The metasoma of one species is mostly dark whereas in the other it is yellow with transverse black stripes.

Bootanelleus sp.
(FIG. 27)

This is a moderate-sized genus of megastigmines characterised by the presence of a medial tooth on the lower clypeal margin and some metallic coloration. There are 20 described species in Australia of which three have been previously associated with seeds of *Casuarina* and galls on *Citrus* and *Microcitrus* (Bouček 1988). The biology of the species reared here from *Fergusonina/Fergusobia* galls is unknown, but it was reared in moderate numbers from three of the seven galls examined (Table 1). Based on these numbers and the fact that it emerged well after all other gall inhabitants, this species is most probably a parasitoid or inquiline. The species is very striking and easy to separate from the other Hymenoptera associated with *Fergusonina/Fergusobia* galls based on its yellow body with bright metallic green dorsal head and mesosoma, black dorsal metasoma and clypeus with a medial tooth (Fig. 27).

Key to the parasitoids reared from *Fergusonina/Fergusobia* Galls in South Australia

1. Fore wing with more than one enclosed cell, moderately complete venation (Figs 7, 11); prepectus absent (Ichneumonoidea) 2
Fore wing with no more than one enclosed cell, venation restricted to anterior margin of wing (Figs 13, 16, 22); prepectus present (Chalcidoidea) 4

2. Fore wing with vein 2mcu present; hind wing with vein r-m meeting Rs after Rs diverges from Sc+R (Fig. 11) (Ichneumonidae) [length about 10 mm without ovipositor; ovipositor shorter than metasoma (Fig. 10); clypeus normal; body orange-yellow with black stripes on metasoma and hind legs (Fig. 9)] (*Poecilocryptus*)............3
Fore wing with vein 2mcu absent; hind wing with vein r-m meeting Rs before Rs diverges from Sc+R (Fig. 7) (Braconidae) [length about 2.5 mm without ovipositor; ovipositor almost as long as body (Fig. 6); clypeus circular and depressed (Fig. 8); orange in colour with posterior mesosoma and metasoma black]........................ ....*Bracon fergusoninus* sp. nov.

3. Hind coxa black; ovipositor about 2.5 x length of hind tibia ....*P. nigromaculatus* Cameron
Hind coxa yellow; ovipositor about 2.2 x length of hind tibia ....*P. galliphagus* Gauld & Holloway

4. In dorsal view, pronotum large and subrectangular or broadly rounded (Figs 20, 21) 5
In dorsal view, pronotum narrow and comprising little if any of dorsal surface of mesosoma (Figs 15, 19)..8

5. Fore wing with elongate stigmal vein (Fig. 17) (Eurytomidae) [body all black, legs often brown or orange-brown distally; female with dorsal mesosoma coarsely reticulate-punctate (Fig. 20), ovipositor short and virtually hidden under metasoma] ....*Eurytoma* spp.
Fore wing with large spot-like stigmal vein (Fig. 22); female with elongate exposed ovipositor (Fig. 25) (Torymidae) 6

6. Body all yellow with some dark markings; clypeus without a medial tooth (*Megastigmus*) 7
Ventral and lateral surfaces of body yellow, dorsal head and metasoma bright metallic green, dorsal metasoma black; clypeus with medial tooth (Fig. 27) ....*Bootanelleus* sp.

7. Metasoma mostly dark dorsally, stripes or striped pattern indistinct ....*Megastigmus* sp. 1
Metasoma yellow with transverse black stripes ....*Megastigmus* sp. 2

8. Hind tarsi 5-segmented (Fig. 24) (Pteromalidae) 9

9. Hind tarsi 4-segmented (Fig. 12) (Eulophidae) 10

9. Body bright yellow or yellow-brown, metasoma depressed, with broad black transverse stripes dorsally; ovipositor short, hardly protruding from posterior metasoma (Fig. 23) ....*Coelocyba nigrocincta* Ashmead
Body bright metallic green; metasoma compressed; ovipositor exserted posteriorly (Fig. 26) ....*Ditropinotella* sp.

10. Body with distinct bright colour pattern, including metallic green markings on dorsal mesosoma (Fig. 14) and black transverse stripes on metasoma ....*Cirrospilus* sp.
Body with uniform dark colour 11

11. Body elongate (Fig. 15), metallic blue-green in colour; dorsal mesosoma with very fine reticulate-puncture sculpturing; fore wing with postmarginal vein about as long as stigmal vein (Fig. 16).......................................*Euderus* sp.
Body relatively short, compact (Fig. 19) and black in colour; dorsal mesosoma with very fine reticulate sculpturing; fore wing with postmarginal vein much longer than stigmal vein (Fig. 18).......................................*Pediobius* sp.

Discussion

The mechanisms by which the host plant cells are induced to proliferate to form a gall remain problematic. Currie (1937) observed that nematodes were actively feeding and causing cell proliferation of plant tissue around the eggs of the fly before they hatched. This suggests that juvenile nematodes are responsible for gall initiation (presumably via salivary secretions). It is not inconceivable, however, that a fraction of oviposition fluid which is injected into the plant by the fly along with the eggs, or mechanical damage by the ovipositor alone, also causes cell proliferation. It has been observed with other *Fergusonina*/*Fergusobia* associations (Davies unpub.) that galls in which fly larvae have died, but in which nematodes are still present, remain green and viable. Currie (1937) reported that when infertile fly eggs were deposited, galls were initiated, but were "aborted at an early stage" while the nematodes persisted for some months but eventually died out. He suggested that further gall growth was attributable to fly larvae. Whatever the mechanism, gall growth for *F. flavicornis* was particularly rapid in that galls attained full size in a matter of weeks during the late summer generation.

While no faecal material was observed in gall cavities of *F. flavicornis*, Currie (1937) observed that faeces were "practically absent" in all but one species of *Fergusonina*. He postulated that nematodes, which by then occur within the fly cavity, feed on fly faeces thus keeping the cavity free of waste. Given the strong stylet of the nematodes, it is more likely that they feed on plant cells. Microscopic examination of specimens cleared in glycerol indicated the presence of a rectum and anus in *F. flavicornis* larvae. It is possible, however, that larvae may store, or produce minimal amounts of excretory products to avoid fouling the cavity. If this is so, it suggests an adaptation similar to that found in the gall-forming Cecidomyiidae (Diptera), the larvae of at least some of which possess a functional anus but produce no noticeable waste products (Gagné 1989). Perhaps related to the storage of waste, *Fergusonina* puparia were observed anchored within the gall cavity by means of a gelatinous substance at the posterior end. It is conceivable that this substance represents digestive waste voided just prior to pupation. Unlike some cecidomyiid galls (Gagné 1989), fungal colonisation of fresh *Fergusonina* galls was not observed. The fly larvae may use the dorsal shield, with its anteriorly directed prongs, to scrape the observed pellets of plant material from the wall of the cavity. Currie (1937) described third instar fly larvae as "tearing down" inner layers of the cavities for food. The shield may also be used to anchor the larvae in one spot within the cavity and to break down parts of the cavity walls prior to pupation to facilitate emergence of the adult fly.

It is unclear how adult flies escape from the galls after emerging from puparia. Dissection of galls revealed that by the time of pupation, cavities on the edges of the gall were separated from the outside only by a thin layer of epidermal cells, suggesting that the larvae tunnel near to the surface prior to pupation. Presumably, adult flies are able to emerge through this thin layer relatively easily. Cavities deeper in the mature gall are separated by thin layers of parenchymatous tissue and sometimes open into each other.

The 12 species of Hymenoptera reared from leaf galls of *F. flavicornis* during this study represent twice the number previously recorded from *Fergusonina* galls. Currie (1937) reared only six species from flower galls in the Canberra area, while Harris (1982) recorded four species from *Fergusonina* galls in India. Further, several species are here associated with *Fergusonina* galls for the first time, viz., *Boucekelleus* sp., *Cirrospilus* sp., *Euderus* sp., *Pediobius* sp., and two species of *Poecilocryptus* (*P. nigromaculatus* and *P. galliphagus*). Although the composition of hymenopteran species associated with individual galls clearly differs, the most common species encountered in this study, *Cirrospilus* sp., *Eurytoma* spp. and *Megastigmus* spp., were reared from all galls (Table 1), while *B. fergusoninus*, *C. nigrocincta* and *Euderus sp.* were reared from more than 70% of galls. The difference in the size of the hymenopteran guild between this study and that of Currie (1937) may be attributable to differences in the structure and position of galls, i.e., *F. flavicornis* forms leaf galls while the species studied by Currie formed bud galls. Also, the fact that galls were caged in the field during this study means that all Hymenoptera were collected, whether they were common or rare. To assess the composition of wasp species by dissecting galls, as apparently undertaken by Currie for at least part of his study, is likely to lead to an underestimation of the true number present. Such dissections mostly reveal larval stages that are often difficult to identify; they are soft-bodied and therefore are easily damaged and there is a greater chance of overlooking rare species.

The leaf galls caused by *F. flavicornis* appear, on dissection, to have a relatively homogeneous matrix and, although some woody tissue is apparent, the most important mortality agent is likely to be parasitic wasps, given that as many individuals of Hymenoptera as *F. flavicornis* were reared from galls (although not all species are necessarily parasitic - see above). However, Currie (1937) attributed up to 60% of *Fergusonina* mortality in bud galls to the inability of fly larvae, prior to pupation, to tunnel through the woody gall tissue induced by hymenopteran inquilines, resulting in their entombment within the gall. He reported that wasp inquilines were found mainly within the outer surface of bud galls, but fly larvae deeper in the gall were largely free of parasites. He also reported that approximately the same number of wasps and flies emerged from leaf galls on *E. Stuartiana* F.v.M. (sic), and suggested that there is a higher level of parasitism in stem tip and leaf tip galls than in flower bud galls.

It is clear from this study and as reported elsewhere (e.g. Boucek 1988; Gough & McMahon 1988) that it is very difficult to determine the biology of gall-associated Hymenoptera. Primarily, this is because their pre-adult stages are hidden within the gall, their biology may change from one stage to another (as in the case of inquilines which may kill the resident gall-former and then become phytophagous), or it may be different from related species that do not inhabit galls. It is therefore naive to assume biological traits for gall-associated wasps by extrapolating from other species or indirect information such as emergence time and/or number of individuals present. For such species, their biology may be determined only by direct and detailed observations including their morphology and life history. In this respect, we have been unable to confirm the biology of any species reared in this study, although we speculate above on what some of these species may be doing, as a means of stimulating further study. The comments made by Currie (1937) that the species of *Ditropinotella*, *Megastigmus* and *Eurytoma* he recorded from *Fergusonina* bud galls are phytophagous must be treated with some caution, given that he presents little or no evidence to support this conclusion, and at least the latter two genera are known to contain species which are either phytophagous or parasitic. Further, his reporting that *C. nigrocincta* is a "true parasite" and that the unknown braconid (probably *Bracon*) he reared was an inquiline is inconsistent with previous studies on these taxa (see above).

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